XXVII. *A brief discussion of A. H. Thayer's suggestions as to the meaning of colour and pattern in insect bionomics.* By Professor Edward B. Poulton, M.A., D.Sc., F.R.S., etc.

[Read October 21st, 1903.]

The discoverer of the meaning of the white under-sides of animals is entitled to a respectful hearing on any question of animal coloration. Furthermore, by his discovery, he has *proved* the benefits which the artist can confer on the naturalist, benefits which we naturalists are only too pleased to receive with gratitude. Our only difficulty is that so few artists seem disposed to consider our problems seriously. In order to be able to do so they must become, at least in spirit, naturalists as well as artists. The more numerous the men of creative power who can occupy, as Mr. Thayer does, the double standpoint, the better it will be for both domains. I therefore express my cordial agreement with Mr. Thayer's claim for the artist. I now propose to make a few comments upon the details of his interesting paper.

Every naturalist will agree that "any coloration or pattern would be conspicuous somewhere." We have often called attention to the fact that colour, pattern, shape, and attitude can only be understood in the natural environment. In fact, Mr. Thayer's own suggestions are, I think, most open to criticism when he is speaking of animals in countries he has not visited; when, for instance, he suggests the kind of concealment brought about by the stripes of the zebra. The lion is the zebra's great enemy, and in spite of their very different kind of colouring they are both adapted to the same general environment. The proportion of dark and light stripes, Francis Galton told us long ago, "is such as exactly to match the pale tint which arid ground possesses when seen by moonlight." So too the suggestion that the groups of similar South American butterflies have gained their resemblance by a common (syncryptic) likeness to some flower which they chiefly frequent would be more plausible if Mr. Thayer had studied them in their native haunts. I have asked Mr.

W. J. Kaye if he can remember the colour of the flowers visited by the black, cow-red, and yellow *Melinæa* group and its mimics in British Guiana, and he tells me they are either white or cream-coloured. Furthermore, Mr. Thayer treats this group as though it were uniform throughout tropical South America, disregarding the extraordinary changes of colour and pattern undergone by its representative species as we pass from one part of the Neotropical region to another. It is almost inconceivable that the following features, which are characteristic of whole groups in particular areas, can be due to the special flowers of those areas. The barred form of Central America, Colombia, and Venezuela, the black hind-wing of the Guianas, the bright yellow band of Eastern Brazil, the chestnut ground-colour of Ega on the Amazon, the black marked fulvous of the Napo River, passing on into the black forms with fulvous marks which constitute so large and characteristic a group in Ecuador, Peru, and Bolivia. In all these cases, nothing short of actual evidence on the spot can warrant the improbable suggestion that we are dealing with syncryptic groups, changing as the species of flowers are replaced by others in passing from one district to another.

Moreover, the theory of a syncryptic resemblance to flowers fails to account for certain broad characteristics of the groups in question, which on the other hand receive a ready explanation on the theory of common warning (synaposematic) coloration. These are (1) the predominance of forms belonging to the sub-families *Ithomiinæ*, with the allied *Danainæ*, and *Heliconinæ*, with the allied *Acræinæ:* (2) the fact that the predominant members of the chief groups in all the other tropical parts of the world are also contributed by the *Danainæ* and *Acræinæ:* (3) the flaunting flight, exposure at rest, and general want of alertness exhibited by the species of these sub-families as compared with others: (4) the more or less exact similarity of the pattern on the under to that on the upper surface, an arrangement comparatively rare in other Rhopalocera: (5) the experimental evidence of the unpalatability of these very sub-families to a large number of the enemies of insects.

Hence, until positive evidence is obtained on the spot in favour of Mr. Thayer's suggestion of syncryptic resemblance, I must regard such an interpretation as highly

improbable, in the case of the groups hitherto explained by the Müllerian or Batesian theories. Of course close syncryptic resemblances between bark-like moths, lichen-like moths, grass-like and pine-needle-like larvæ, etc., have been known and admitted for many years.

Leaving the tropics we find a beautiful example of mimicry, Batesian, or more probably Müllerian, which has arisen in Mr. Thayer's own region, and has never wandered much beyond it, an example moreover very well known to the American artist-naturalist, viz. the resemblance of the northern *Limenitis* (*Basilarchia*) *archippus* (*misippus*) to the Danaine intruder from the tropical south, *Anosia plexippus*.

In this case there is little doubt that the Nymphaline has been actually drawn away from an ancestral appearance, much like that now borne by *L. arthemis*, explained by Mr. Thayer as promoting concealment by likeness to flower-masses and their background. If therefore Mr. Thayer is compelled to admit all this effect produced by the Danaine intruder in his own northern region, why should he not be ready to accept far more extended effects of the same kind in the crowded luxuriant life of the tropics?

I do not think that naturalists *have* so entirely misunderstood the principle of a cryptic pattern resembling some object in the environment combined with the effacive gradation so admirably explained by Mr. Thayer. His illustrations of tiger, lion, brilliantly-coloured fish, appearance of forest and shore birds, etc., all these are accepted at once and have been accepted for a long time. But naturalists have regarded the skunk as conspicuous, and I feel sure that Mr. Thayer will admit that it falls into another category from that which includes the forms just named. If concealment is brought about by the beautiful and delicately adjusted effacive gradation from upper dark to under white, as is now generally admitted, surely the "slight amount of effacive gradation" of the black skunk cannot be the same thing, or belong to the same class.

We must admit Mr. Thayer's main conclusion, that the forms we call conspicuous might be more conspicuous, and also accept the statement that a pattern is less conspicuous than the monochrome.

Admitting all Mr. Thayer says, at least of the butterflies

he knows in the living state, and of the skunk, he cannot contend, I think, that his criticisms are powerful enough to transfer these examples into the bionomic group which contains the well-known examples of cryptic colouring—the skunk into the same category as the hare or ptarmigan, the under-side colouring of the Danaine butterflies, or the Nymphaline genus *Limenitis* (*Basilarchia*) into the same category with that of *Grapta* or *Kallima*, etc. I believe the whole of his criticism of warning colours can be accepted, and can be reconciled with the existing hypotheses. All animals with warning colours have enemies, all are liable to special attacks, in times of exceptional hunger, by enemies which would at other times neglect them. Even the skunk has special bird enemies. Provided such forms are easily seen and avoided by enemies which respect their special modes of defence, it is clearly an advantage to be as far as possible concealed from those which do not respect them. Hence conspicuousness, but, as Mr. Thayer tells us, something very far short of ideal conspicuousness. The black and white pattern of the skunk is probably glaring and conspicuous enough to all enemies near at hand, but at the immense distance covered by the long-range sight of a predaceous bird it may melt into an inconspicuous grey.

The same kind of interpretation probably holds for a cryptic element whenever it exists in the appearance of butterflies belonging to distasteful sub-families. It is the probable meaning of the transparency so widespread in the *Ithomiinæ*, although I do not think it is so effective in concealing as Mr. Thayer supposes. We must remember that many of these transparent species are excessively abundant, flying in clouds often made up of the individuals of several species and different genera. I quite recognize that the transparency may protect such forms against distant enemies, but I should be much surprised if the species of *Methona* and *Thyridia*, as well as *Dismorphia orise*, of which they are the models, are not rendered extremely conspicuous to enemies close at hand, by their numbers, habits of flight, and attitudes of rest. As Mr. Thayer has said, the black and white markings will melt into an elusive grey on a rapidly vibrating wing ; but the specially protected groups have developed a sailing flight which shows off the elements of pattern to perfection. When the body in such groups is effacively graded the

explanation may well be that it is advantageous to direct attention to the wings rather than the vital parts; but it is precisely in these groups that the black body, and sometimes the head, are so often marked with white or red. A bright red or orange collar is found in several species. Furthermore, it must be remembered that the body being moved much less rapidly than the wings during flight is more easily seen. The black and white apical area of the fore-wing may help to conceal, as Mr. Thayer supposes, under certain conditions, but the numerous examples of injuries at this very spot, figured in Plates IX and XI of our Transactions for last year, strongly support the hypothesis that it is directive, and diverts the stroke of the attacking enemy from the body.

Apart from the suggested interpretation of mimetic resemblance, which I believe to be untenable, Mr. Thayer's suggestions supplement and complete rather than oppose existing hypotheses. The words he uses of the wasp may in fact be employed of the skunk, and the well-known distasteful Rhopalocerous groups, etc. The colours may not be conspicuous to enemies at a great distance, "yet when seen they may well profit by the pattern's recognizability." We have rather insisted on this latter fact and its advantage, and Mr. Thayer has done us good service in calling attention to the other aspect of the appearance.

Ideas not dissimilar to those of Mr. Thayer's upon warning colours have for some time crossed my mind. Thus last year I suggested as regards the abundant, much-mimicked *Limnas chrysippus*, that its desert form *dorippus* (*klugii*) "is a development in a procryptic direction in areas where the struggle" is especially severe (Trans. Ent. Soc. Lond., 1902, p. 475).

Furthermore, the idea has often forced itself upon me that the ground colour of the type form of this butterfly, as well as of the Ethiopian *Acræinæ* and Lycid beetles, may, under certain conditions and at a certain distance, become procryptic against the prevalent reddish tinge of the soil of Africa.

The author's suggestions of the resemblance of butterfly patterns in general to flower-masses and the shadow-depths between them; of the under-sides of *Grapta* and the upper-sides of many moths representing dead leaves lying on the ground and casting such shadows as they would throw at their small distance from it; of the concealing

effect of iridescence ; of the overflow of individuals from a concealing region into one less favourable—in all these we have illuminating ideas which demand the fullest and most respectful consideration. That they are sound principles must, I think, be admitted at once ; but their relative importance, the amount of ground which they cover, cannot be decided offhand. I would only point out the extraordinary frequency with which a continuous black colouring unrelieved by pattern is accompanied by iridescence or surface colours of some kind. In view of the whole drift of Mr. Thayer's interesting and most suggestive paper it becomes probable that dead black would be *too* conspicuous even to many a well-armed aculeate or nauseous *Euploea*, and that it is therefore modified so that it obtrudes less upon the distant view of enemies which "mean business."

Although I have criticized some of the details of Mr. Thayer's paper, I should wish again to point out that they concern just those species which have not come under his own eyes in the living state. Naturalists owe him a large debt for the many new points of view and illuminating suggestions contained in his memoir.

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